

High fire frequency and the impact of the 2019–2020 megafires on Australian plant diversity

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Abstract

Aim: To quantify the impact of the 2019–2020 megafires on Australian plant diversity by assessing burnt area across 26,062 species ranges and the effects of fire history on recovery potential. Further, to exemplify a strategic approach to prioritizing plant species affected by fire for recovery actions and conservation planning at a national scale.

Location: Australia.

Methods: We combine data on geographic range, fire extent, response traits and fire history to assess the proportion of species ranges burnt in both the 2019–2020 fires and the past.

Results: Across Australia, suitable habitat for 69% of all plant species was burnt (17,197 species) by the 2019–2020 fires and herbarium specimens confirm the presence of 9,092 of these species across the fire extent since 1950. Burnt ranges include those of 587 plants listed as threatened under national legislation (44% of Australia's threatened plants). A total of 3,998 of the 17,197 fire-affected species are known to resprout after fire, but at least 2,928 must complete their entire life cycle—from germinant to reproducing adult—prior to subsequent fires, as they are killed by fire. Data on previous fires show that, for 257 species, the historical intervals between

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fire events across their range are likely too short to allow regeneration. For a further 411 species, future fires during recovery will increase extinction risk as current populations are dominated by immature individuals.

Main conclusion: Many Australian plant species have strategies to persist under certain fire regimes, and will recover given time, suitable conditions and low exposure to threats. However, short fire intervals both before and after the 2019–2020 fire season pose a serious risk to the recovery of at least 595 species. Persistent knowledge gaps about species fire response and post-fire population persistence threaten the effective long-term management of Australian vegetation in an increasingly pyric world.

KEYWORDS

biodiversity assessment, bushfires, conservation biogeography, conservation planning, extreme events, fire ecology, megafires, plant conservation, plant diversity, rapid assessment

1 | INTRODUCTION

During the 2019–2020 bushfire season, approximately 10,300,000 ha of the Australian landscape burned (Figure 1a). Outside arid regions of the continent, fires of this magnitude are unprecedented in contemporary Australian fire history (Nolan et al., 2020; Shine, 2020). The impact of the megafires on Australian biota has been widespread, including rapidly assessed losses to key populations of threatened fauna (Ward et al., 2020). Yet, it is the vegetation of Australia, which forms the critical foundation for terrestrial biota, providing key resources such as food and shelter, which translate to the growth, reproduction and survival of species by, for instance, creating nesting sites and protection from predation (Haslem et al., 2011; Keith, 2017).

Plants—aside from their crucial importance to higher trophic groups—are among the most hyper-diverse organisms on Earth with recent estimates of up to 390,000 taxa globally (Antonelli

et al., 2020). Australia has approximately 26,000 nationally accepted plant taxa (species, subspecies, varieties—hereafter “species”) representing 6% of the world's plant richness (Australian Plant Census (APC), June 2020). Further, up to 88%–92% of Australian plant species occur nowhere else globally (Chapman, 2009; Gallagher et al., 2020), making the impact of the 2019–2020 fire season on Australian plant species a matter of global significance for plant conservation.

Here, we report on the national response to prioritizing the effects of the 2019–2020 megafires on Australian plant diversity in research commissioned by the Australian government. The results were part of a broader effort to assess and respond to the effects of the fires on biodiversity, which was led by the Wildlife and Threatened Species Bushfire Recovery Expert Panel, chaired by the Threatened Species Commissioner. The Expert Panel used the analyses presented, as well as information on other threats such as disease risk and herbivore impacts (Gallagher, 2020), to provide

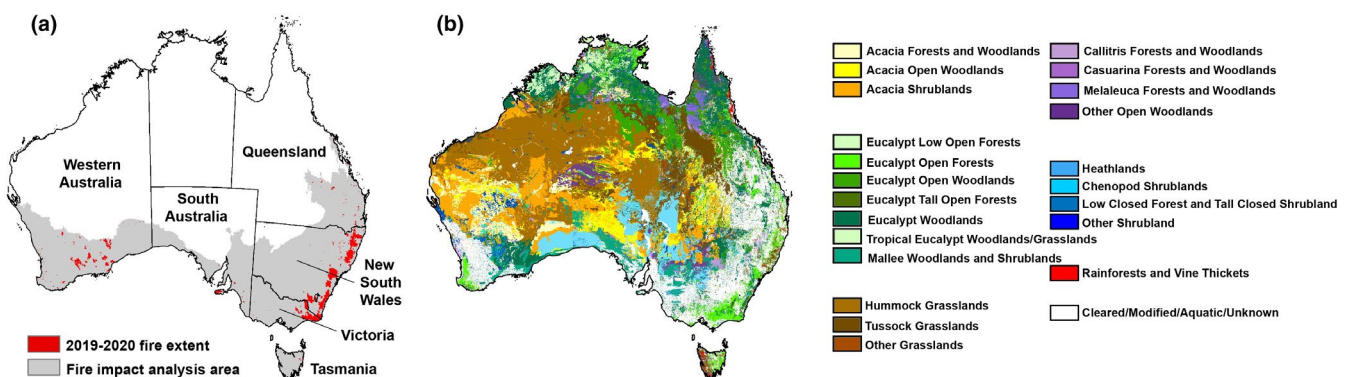


FIGURE 1 (a) Spatial extent of areas burnt in the 2019–2020 bushfires (red areas) across 43 bioregions from the Interim Bioregionalisation of Australia (IBRA) considered most at risk of impact (grey areas). Data sourced from the National Indicative Aggregated Fire Extent Database (NIAFED); (b) Australia's Major Vegetation Groups (MVGs) according to the National Vegetation Inventory System (version 5.1). MVGs have been grouped into simplified vegetation units (e.g., Acacia-dominated) and coloured using similar hue. For simplicity, six MVGs were grouped into a single map unit (white): cleared, non-native vegetation, buildings; inland aquatic—freshwater, salt lakes, lagoons; naturally bare—sand, rock, claypan, mudflat; mangroves; regrowth, modified native vegetation; sea and estuaries; unclassified forest; unclassified native vegetation; unknown/no data.

strategic advice on actions needed to support the post-fire recovery of Australian plants. The implementation of a national approach to prioritizing species in response to the Australian fire crisis offers a template for responding to subsequent fire crises, which will continue to emerge globally.

Australia's c. 26,000 plant species encompass 260 families and 2,244 genera, several of which are notable for their evolutionary distinctiveness and ecological strategies. For instance, the family Proteaceae has a large radiation of species in Australia ($n = 1,590$) almost half of which ($n = 729$ species) belong to 39 entirely endemic genera (APC, June 2020; accessed at <https://biodiversity.org.au/nsl/services/apc>). Vegetation formations encompass a broad range of physiognomic variation (Figure 1b). Regionally, several areas of high plant endemism and evolutionary significance are recognized, including the Southwest Australian Floristic Region (SWAFR) in Western Australia and the East Coast World Heritage Areas including the Greater Blue Mountains and Gondwanan Rainforests (Hopper & Gioia, 2004; Keith, 2004). Species in these regions—and the Australian flora more broadly—exhibit a range of traits associated with selective pressures imposed by repeated abiotic and biotic disturbance over deep time (Gill, 1975). Foremost among these pressures is fire—a disturbance that has shaped the distribution and diversity of Australian vegetation since the mid-Tertiary (~30 MYA) (Attiwill & Wilson, 2003).

Many extant Australian plant species are adapted to specific fire regimes through their exposure to burning on evolutionary time scales (Miller & Murphy, 2017; Williams et al., 2012). Evidence from the palaeorecord indicates the increasing presence of charcoal and particulate matter in the Australian landscape from the mid-Tertiary (Lynch et al., 2007) and the parallel emergence of fire-adapted vegetation. The importance of fire in shaping plant form and function has been corroborated by evidence from macrofossils (Carpenter et al., 2015; Hill et al., 1999), palynology (Martin, 1994) and molecular markers (Crisp et al., 2011), which indicate adaptive radiations in key traits. For instance, traits associated with fire response—such as serotiny and epicormic resprouting—first emerged in Australia during the Eocene (80 MYA) coinciding with pulses of increased fire activity (Crisp & Cook, 2013). Since this time, traits associated with adaptation to fire have arisen throughout the Australian flora resulting in many extant species, which can not only regenerate after fire but are also reliant on fire to complete essential phases of their life cycle (Auld & O'Connell, 1991; Auld & Ooi, 2017). This tight coupling between plant demographic processes, such as mortality and recruitment, and fire emphasizes the importance of the frequency of fire in shaping Australian vegetation (Gill, 1975; Keith, 1996).

Different components of the fire regime may have adverse impacts on plant persistence, including fire frequency, severity, seasonality, type and spatial extent and patchiness. It is critical to assess the impacts of any major wildfires on plant species against how they are impacted by the components of the fire regime and their interactions (Williams et al., 2012). Here, we focus on the impact of high fire frequency, which has been previously shown to threaten the persistence of plant species reliant on specific intervals between

fire across their range to facilitate regeneration (Fisher et al., 2009; Russell-Smith et al., 2002). The abundance and dominance of woody species in plant communities typically decrease through long-term exposure to repeated short intervals between fires (Cary & Morrison, 1995; Gill, 1975). Short temporal intervals between fires can also disrupt the replenishment of seed banks, which are essential to post-fire recruitment and population persistence, particularly in obligate seeders (species that lack regenerative organs and rely entirely on seed germination for post-fire recovery) and resprouters (species with the capacity to generate new shoots from dormant buds post-fire) that suffer high mortality rates (Auld & O'Connell, 1991; Auld & Ooi, 2017; Russell-Smith et al., 2002).

The time required to replenish seed banks post-fire varies between species and across time and space, though a fire-free period of at least 15 years between successive fires, is needed for many woody species (Keith, 1996), particularly narrow ranged endemics, which may lose all standing individuals in a single fire event (Auld, 1996). Sufficient fire-free intervals ensure that seed banks are adequately replenished to maintain future post-fire populations (Auld et al., 2000; Enright & Lamont, 1989). Some species—such as shrubs and trees in low productivity environments like the mallee and Great Western Woodlands—may require longer fire-free periods (Gosper et al., 2013). For others, an absence of fire for 50 years or more is needed to maintain populations (Bowman, 2000). Such fire-sensitive species have a limited capacity to regenerate after fire, making them vulnerable to decline or local extinction if burnt across their entire range. This includes slow-growing tree species lacking seed banks but with some capacity to resprout basally and epicormically, but whose whole trunks are often killed in severe fires forcing plants to regrow from below ground (Bowman, 2000).

Short intervals between fires may also kill juveniles of resprouting plants before they become large enough to survive subsequent fires (Gill & McCarthy, 1998; Keith, 1996). The species that are most susceptible to these risks are resprouters that are slow-growing, slow to develop protective or regenerative structures (i.e., thick bark, lignotubers, rhizomes) or slow to replace mortality due to low fecundity (Keith, 1996). Further, widespread and cumulative loss of mature plants, which are obligate seeding, exposes species to risks associated with recruiting new individuals to replace those lost. These risks include susceptibility to future fires before populations replenish seed banks, stochastic post-fire events and recruitment failure driven by higher seedling susceptibility to other threats such as grazing, weeds or pathogens (Auld et al., 2020; Gallagher, 2020).

Projected changes to fire conditions under future climates (Abatzoglou et al., 2019; Bowman et al., 2020) may expose many plant species to “interval squeeze”—a narrowing the favourable interval between fires, hence increasing local extinction risk by accelerating demographic processes associated with population decline (Enright et al., 2015). Fire management practices which repeatedly target particular locations or regions place species requiring specific fire-free intervals—such as obligate-seeding species—at risk of local or global declines or extinction (Fisher et al., 2009; Ooi et al., 2006; Russell-Smith et al., 2002).

State-based environmental legislation in Australia recognizes the significant risk associated with adverse fire regimes on the persistence of species, populations and ecological communities. For instance, in New South Wales (NSW) the ecological consequences of high-frequency fires are listed as a Key Threatening Process under the *NSW Biodiversity Conservation Act (2016)* (BC Act) and fire-free thresholds for threatened species are used to inform bushfire planning (Cheal, 2010; https://www.rfs.nsw.gov.au/_data/assets/pdf_file/0014/24332/Bush-Fire-Environmental-Assessment-Code.pdf).

In this study, we quantify the impact of the 2019–2020 megafires on the ranges of all 26,062 recognized Australian plant species and assess recovery potential based on fire history. We use spatial intersects of geographic ranges and the national extent of the megafires (not only the south-east of the continent), and specifically explore effects on threatened and endemic species, plant families and major vegetation groups. We assess the recovery potential of species with reference to previous fire history by collating data on two key plant attributes: (1) fire response (resprouting or obligate seeding), and (2) growth form (woody or non-woody) and then combined this knowledge with spatial data on the extent of fires in each fire season between 1969–2018.

2 | METHODS

All analyses were carried out in R (R Core Team, 2013), using the packages *raster* (Hijmans et al., 2013), *fasterize* (Ross, 2018), *sf* (Pebesma, 2018) and *V. Phylomaker* (Jin & Qian, 2019). Spatial layers were projected to a common equal-area coordinate system prior to analysis (Australian Albers; EPSG: 3577). Taxonomy follows the APC. The study region for analysis—hereafter the “fire impact analysis area”—comprised 43 bioregions in the Interim Bioregionalisation of Australia (IBRA) considered most at risk from the 2019–2020 fire season by the Wildlife and Threatened Species Bushfire Recovery Expert Panel convened by Department of Agriculture Water and Environment (DAWE) in January 2020. These bioregions cover 29% of Australia and are concentrated in the southern half of the continent (grey polygon in Figure 1a).

2.1 | Fire extent

The spatial extent of the 2019–2020 fires was quantified using the National Indicative Aggregated Fire Extent Dataset (NIAFED; <https://data.gov.au/dataset/ds-environment-9ACDCB09-0364-4FE8-9459-2A56C792C743/details?q=>; Figure 1a; DAWE, 2020a). The NIAFED is a spatial polygon layer produced by DAWE in rapid response to the bushfire crisis and provides the most comprehensive national dataset of the fire extent. The NIAFED was masked to include only the fire impact analysis area. Polygons were rasterized to a 250 m grid cell resolution, and the proportion of 1,600 × 250 m cells burnt in each 10 km cell was quantified.

The annual spatial extent of fires between September–March in each year (1969–2018) was quantified by combining data from remote sensing and state agency fire history databases. Remotely sensed data on fire extent in each season between 2003–2016 were accessed from the Global Fire Atlas <https://www.globalfiredata.org/fireatlas.html> (Andela et al., 2019), and—using the same methods—fire extent data were created for the 2017 and 2018 seasons using imagery from the MODIS product (MCD64A1). Alternate data on annual fire extent were accessed under licence from environment agency databases in three Australian states—New South Wales (NSW National Parks and Wildlife Service Fire History—Wildfire and Prescribed Burns dataset <https://data.nsw.gov.au/data/dataset/1f694774-49d5-47b8-8dd0-77ca8376eb04>), Western Australia (Western Australian Department of Biodiversity, Conservation and Attractions Fire History dataset (1969–2020)) and Victoria (Victorian Department of Environment, Land, Water and Planning Fire History dataset). All these datasets have known issues regarding completeness and reliability; for instance, in non-forested areas of Western Australia (WA) (e.g., Great Western Woodlands, arid zone and South Coast) precise dates of fire are unknown for the period 1969–70 and overall coverage of fire history mapping is likely to be less accurate on private lands and non-forest areas. Remotely sensed data and agency mapping of fire extent were combined to provide an inclusive estimate of the history of fires in Australia over the last 50 years.

Data on fire extent were combined with species range data to estimate the impact of the 2019–2020 fires and preceding fires on Australian plant species.

2.2 | Species range data

The ranges of 26,062 plant species with accepted names in the APC in June 2020 were defined using two alternate approaches: (1) point-based, where location data (latitude and longitude coordinates) from digitized herbarium specimens were used to estimate range; and (2) polygon-based, where species distribution modelling (SDM) and range mapping approaches were used to identify areas of suitable habitat across Australia. Digitized specimen records were accessed via the Atlas of Living Australia (ALA) Web Service (<https://api.ala.org.au/>; <https://doi.ala.org.au/doi/10.26197/ala.996c4566-1829-4bdf-9f7d-3c729007e208>). Raw herbarium records were refined by removing taxonomic errors (misspellings, synonyms) and spatial inaccuracies and outliers using a cleaning workflow in R (Gallagher et al., 2019). We retained 2,498,598 records with valid latitude and longitude coordinates collected in or after 1950 (median per species = 46 records, range = 1–2,710 records).

Poisson point process modelling (PPPM), range bagging, area of occupancy (AOO) calculation and pre-existing mapping of Species of National Environmental Significance (SNES; <https://www.environment.gov.au/science/erin/databases-maps/snes>) were used to create polygons of potentially suitable range for each species using a suite of packages in R (Appendix S3). The choice of range mapping technique was contingent on the number of unique cells

occupied by a species in the cleaned occurrence data; taxa with ≥ 20 cells ($n = 18,576$), 10–20 cells ($n = 2,474$) and < 10 cells ($n = 3,726$) were modelled using PPPM, range bagging and AOO, respectively. Note that SNES maps were used as the sole source of range data for all species listed as threatened on the *Commonwealth Environment Protection and Biodiversity Conservation (EPBC) Act* ($n = 1,335$ species). Some species recognized in the APC did not have any associated data on their geographic range.

PPPMs were created using regularized down-weighted Poisson regression based on 20,000 background points at a 10 km \times 10 km grid cell resolution and calibrated using the range modelling workflow of the BIEN database (<https://biendata.org/methods.php>; Maitner et al., 2018). PPPMs were calibrated on mean annual temperature ($^{\circ}\text{C}$), mean diurnal temperature range ($^{\circ}\text{C}$), annual precipitation (mm), precipitation seasonality (coefficient of variation), annual mean radiation (AMR; W/m^2), aridity index, bedrock depth (m), soil bulk density (fine earth) in kg/m^3 , clay mass fraction (%), silt mass fraction (%) and soil pH. Spatial predictions of range were made only in ecoregions (Dinerstein et al., 2017) where the species had been previously recorded to reduce commission error. Climate and soil data were accessed from WorldClim2 (Fick & Hijmans, 2017), the Global Aridity and PET database (Trabucco & Zomer, 2018), CliMond (Kriticos et al., 2012) and the International Soil Reference and Information Centre (Hengl et al., 2017).

PPPMs were fit with a combination of features (i.e., linear (all species), quadratic (species with > 100 records), product (species with > 200 records) and fivefold spatially structured cross-validation). The regularization parameter in PPPMs was determined as the value, which was 1 standard deviation below the minimum deviance based on 10-fold cross-validation (Hastie et al. 2009). The five models for each species were combined to create one unweighted ensemble of continuous prediction values that were converted to presence/absence predictions using a threshold, which reserved the 5th percentile of the ensemble predictions at presence locations used to train models. Area under the curve (AUC) was used to assess performance; PPPM models had a mean test AUC of 0.81 (s.d. 0.16).

All resulting occurrence data (point locations) and range maps (polygons) were intersected with the NIAFED layer to calculate the percentage of the species range burnt in the 2019–2020 fires.

2.3 | Threatened and endemic status

We examined the specific impact of the 2019–2020 fires on plant species listed as threatened at the state, territory or national level and those endemic to a particular state or territory. A list of species listed as threatened under Australian state, territory or commonwealth legislation was accessed from the Species Profile and Threats Database (SPRAT) in June 2020. Appendix S1 provides details of all legislation considered. A list of species endemic to a particular state or territory was collated using distribution information associated with the APC accessed via the National Species List portal (<https://biodiversity.org.au/nsi/services/export/index>).

2.4 | Major vegetation groups

We quantified the extent of burnt area across all of Australia's Major Vegetation Groups (MVGs; $n = 28$; Figure 1b). Spatial data on MVGs were accessed from the National Vegetation Information System (ver. 5.1, present theme) and intersected with the NIAFED layer to estimate the extent of fire in each vegetation type across the analysis area.

2.5 | Species historical exposure to fire

To assess how fire history may shape species' capacity to recover from the 2019–2020 fire season, we developed prioritisation criteria to classify species into four levels of risk: "high," "medium," "low" and "none." These criteria focussed on two pathways to decline: (1) the impact of high fire frequency (short intervals between fire); and (2) cumulative exposure to fire risk for immature individuals in plant populations. The high fire frequency analysis examined the impact of antecedent fire intervals on recovery potential across all species, whereas the cumulative exposure analysis concerned obligate-seeding species only. In all analyses, occurrence data (point locations) and range maps (polygons) were assessed independently, and species were placed into the highest category of risk identified across both sources as a precautionary measure.

For high fire frequency, species were divided into two groups—woody and non-woody—and assigned a "high" risk rating where $\geq 25\%$ of the range was burnt in 2019–2020 and fire history data indicated one or more previous fires occurred in this burnt area within the past 5 years (non-woody species) or the past 15 years (woody species) (Figure 2). All other species were assigned to the risk categories "medium," "low" and "none" by varying the threshold for range burnt as follows: medium— $\geq 10\%$ to $< 25\%$, low— $> 0\%$ to $< 10\%$, and none—no known sites or habitat burnt in the 2019–2020 fires. Growth form data for all species were obtained from the AusTraits database (Falster et al., 2021) and used to characterize species as "woody" or "non-woody" as follows: non-woody—herbs, graminoids, epiphytes, parasites, palms, herbaceous climbers, ferns and geophytes ($n = 12,867$); and woody—trees, shrubs, subshrubs and lianas ($n = 13,195$). For a small subset of woody tree species ($n = 463$ species), any fire in the last 50 years was considered to place the species at "high" risk of decline or extinction. These fire-sensitive trees typically occupy rainforests and with no (or small) soil or canopy seed banks and no known capacity to recover through resprouting.

By contrast, for cumulative exposure to fire risk, we focused solely on species known to be obligate-seeding (killed by fire) or fire-sensitive trees, which were burnt to some extent in the 2019–2020 fires. These species were considered at high risk of population declines or local extinctions, where a large proportion ($\geq 50\%$) of their point locations or range polygons were predicted to comprise immature plants at the time or after the 2019–2020 megafires on the basis that the antecedent fire interval was shorter than their primary juvenile period. To estimate this, we

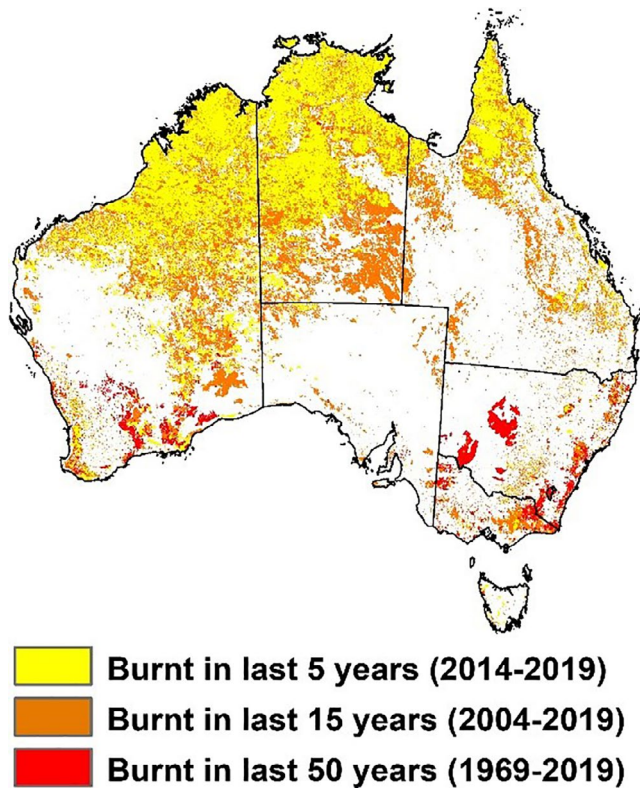


FIGURE 2 Fire history mapping for three intervals (areas burned in the last 5, 15 or 50 years) according to remotely sensed mapping of fire extent from the Global Fire Atlas and spatial polygons of fire extent in Australian state environmental agencies. White areas have not been burnt in the last 50 years according to the data sources accessed

summed the percentage of the range burnt in 2019–2020 with the percentage of sites outside the fire impact analysis area and affected by one or more fires in the last 5 years (non-woody species), 15 years (woody species) and 50 years (fire-sensitive trees). Species at medium and low risk of population declines had 30%–50% and 0%–30% of their point locations or range polygons predicted to comprise immature plants at the time of the 2019–2020 megafires, respectively. Data on obligate seeding were accessed from AusTraits using data from 24 studies (see <https://traiteco-evo.github.io/austraits.build/> for access). These studies included 15,256 fire response observations across 9,778 species, with 1–13 unique entries per species. Species were categorized as “consensus fire killed” if they were universally recorded as “fire killed” in AusTraits and as “almost always fire killed” if at least 75% of data entries in AusTraits indicated they were “fire killed.”

3 | RESULTS

Between 36%–69% of all Australian plant species (9,092–17,197 species) had some part of their geographic range burnt during the 2019–2020 season within the fire impact analysis area (Table 1; see

Figure 1a for analysis area). That is, suitable habitat identified in range maps for 17,197 plant species was burnt (69% of all species) and point locations from herbarium specimens confirm the recent presence of 9,092 of these species within the fire extent. Frequency distributions of the percentage of range burnt are approximately Gaussian (Figure 3a), although the inclusion of species with >0% to <0.1% of their range burnt introduced considerable left skew for the range mapping data (Figure S1). Most Australian plant species had burnt area percentages at or below the 50th percentile of the distribution ($n = 8,575$ – $16,604$ species; Figure 3a).

The percentage of endemic, fire-affected plant species varied between Australian states (Table 1); NSW had the highest number of endemic species with range burnt ($n = 956$ – $1,152$ species), which is 77%–92% of the state's 1,320 endemic plants. This reflects the large geographic extent of the fires in NSW. Some notable areas of high plant endemism—such as Kangaroo Island in South Australia and the Stirling Ranges in Western Australia—were also burnt in the fires, contributing to localized losses of standing populations and individuals of species found nowhere else globally. These endemics include several species whose adult plants are killed by fire, which will be reliant on post-fire recruitment to recover, such as the herb *Irenepharsus phasmatodes* Hewson (Kangaroo Island cress) and the shrubs *Banksia montana* (C.A. Gardner ex A.S. George) A.R. Mast & K.R. Thiele (Stirling Range dryandra) and *Andersonia axilliflora* (Stschegl.) Druce (giant andersonia).

Nationally, between 90–153 plant species had >90% of their range burnt when considering each source of range data—range maps and point locations—independently. However, 190 species were burnt across >90% of either their mapped range or point locations. Of these 190 species, 20 had all their mapped range and point locations burnt (i.e., 100% range burnt—e.g., *Callistemon forresterae* Molyneux Figure 3b, *Acacia alaticaulis* Kodala & Tindale Figure 4b). A further 517–593 species had >50% of their range burnt ($n = 784$ assessing both sources combined), including species with relatively large range sizes (e.g., the sedge *Lepidosperma limicola* N.A. Wakef.; c. 132,000 sq km) and narrow-ranged endemics (e.g., the shrub *Dracophyllum oceanicum* E.A. Br. & N. Streiber; 322 sq km).

3.1 | Impact across taxonomic groups

The impacts of the 2019–2020 fire season were spread widely across the taxonomic diversity of Australian plants (Figure 3c). In total, 31% of Australian plant families had more than 50% of their species burnt ($n = 81$ of 263 families). Between 42%–79% of species in Australia's ten largest plant families (55% of all species richness) were burnt somewhere across their range (Table 2; Figure 3c). This includes 79% of species in the Proteaceae, and 65% and 67% of all Fabaceae and Myrtaceae species, respectively (Table 2). The 190 species with >90% of their range burnt were drawn from a range of genera ($n = 79$) and families ($n = 29$), including *Grevillea* ($n = 13$ species), *Hibbertia* ($n = 13$ species), Myrtaceae ($n = 39$ species) and Proteaceae ($n = 23$ species).

TABLE 1 Impact of the 2019–2020 fire season on the ranges of Australian plant species

Species group	Species (n)	Any range burnt species (%)	Any range burnt (count)	>species with 90% range burnt (% of species)	>species with 50% range burnt (% of species)	>species with 30% range burnt (% of species)
All species	26,062	36%–69%	9,092–17,197	90–153 (<1%)	517–593 (3%)	1,319–1,461 (5%–6%)
Threatened in						
Australia (EPBC Act)	1,335	44% ^a	587 ^a	35 (3%) ^a	90 (7%) ^a	148 (11%) ^a
New South Wales	700	59%–91%	386–598	32–34 (5%)	79–107 (12%–16%)	139–199 (21%–30%)
Western Australia	436	13%–51%	56–220	1–2 (<1%)	4–12 (1%–3%)	24–25 (6%)
Victoria	1,770	60%–93%	963–1,499	17–18 (1%)	76–95 (5%–6%)	229–249 (14%–15%)
South Australia	807	53%–87%	404–665	3–4 (<1%)	19–21 (2%–3%)	34–40 (4%–5%)
Queensland	935	15%–43%	138–387	0–2 (<1%)	3–14 (<1%)	31–38 (3%–4%)
Tasmania	460	59%–79%	257–344	0–1 (<1%)	2 (<1%)	14–24 (3%–6%)
Australian Capital Territory	13	31%–85%	4–11	0–1 (0%–8%)	0–1 (0%–8%)	1–2 (8%–15%)
Endemic to						
New South Wales	1,320	77%–92%	956–1,152	52–104 (4%–8%)	306–311 (25%)	519–626 (42%–50%)
Western Australia	8,952	32%–68%	2,754–5,822	4–10 (<1%)	40–45 (<1%)	98–190 (1%–2%)
Victoria	408	32%–80%	113–278	12–13 (3%–4%)	28–31 (8%–9%)	43–57 (12%–16%)
South Australia	488	31%–70%	160–319	3–6 (0%–1%)	37–38 (8%)	56–58 (12%–13%)
Queensland	3,629	11%–54%	388–1,865	1–3 (<1%)	3–11 (<1%)	19–30 (<1%)
Tasmania	543	9%–77%	49–402	0 (0%)	0 (0%)	1–2 (<1%)
Australian Capital Territory	6	33%–83%	2–5	0 (0%)	1 (17%)	1 (17%)
Non-threatened or endemic	7,976	40%–65%	3,203–5,197	2–6 (<1%)	23–71 (<1%)	216–342 (3%–4%)

Note: Burnt area intersects were based on the fire extent data from the National Indicative Aggregated Fire Extent Database (NIAFED). Data on the spatial extent of species ranges were sourced from point locations associated with digitized herbarium records and range maps. Range maps were derived from distribution modelling (point-process models, range bagging), area of occupancy (AOO) estimates and—for species listed as threatened on the *Environment Protection and Biodiversity Conservation Act*—Species of National Environmental Significance mapping. The counts and percentages of affected species are presented as a range of values to reflect the use of two sources of distribution data (point locations and range maps). Note species may appear in multiple groups if listed as threatened in more than one jurisdiction.

^aOnly SNES mapping was used to assess the extent of burnt area across threatened species listed on the EPBC Act.

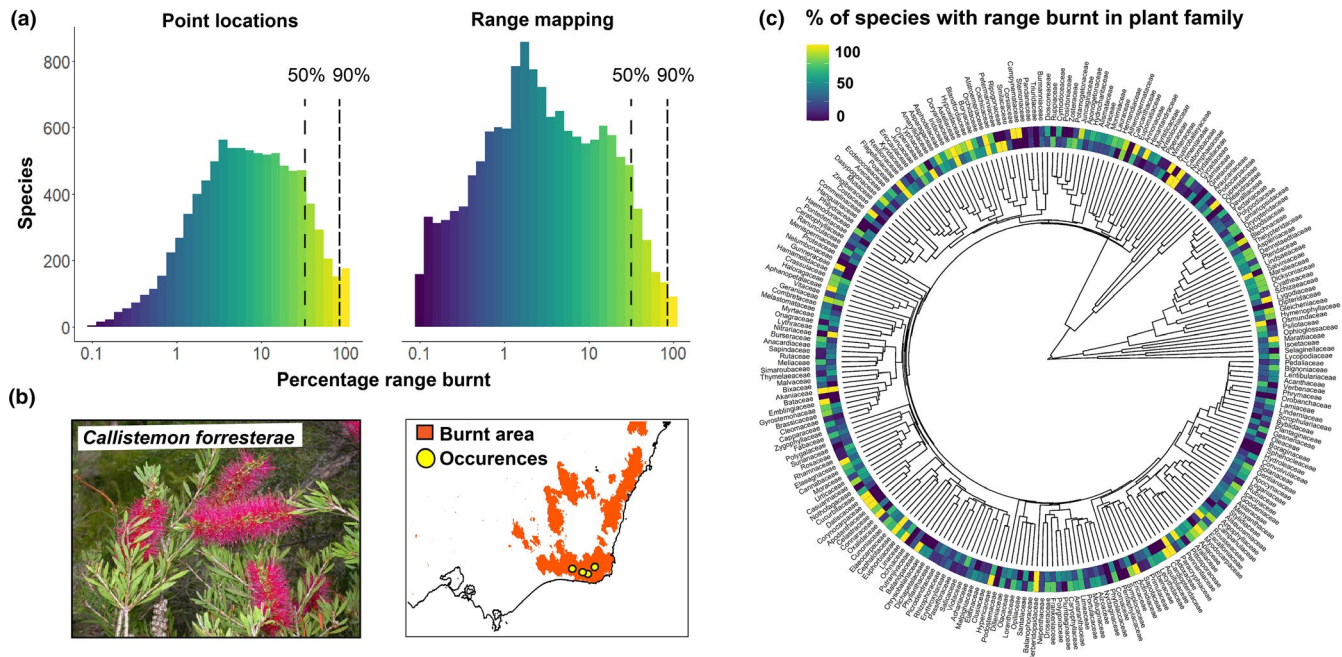


FIGURE 3 Impact of the 2019–2020 fire season on all Australian plant species and families. (a) Frequency distributions of the percentage of range burnt across species. Estimates of the extent of the range burnt for each species are derived from point locations associated with digitized herbarium records (left) and range maps (right) derived from point-process models, range bagging and area of occupancy (AOO) estimates, all of which were intersected with the National Indicative Aggregated Fire Extent Database (NIAFED). Lines show the 50th and 90th percentiles of the raw data, and distributions exclude species with $>0\%$ but $<0.1\%$ of their range burnt (i.e. 10 species for point locations; 2,564 species for range mapping; see Figure S1 for full distributions). (b) A exemplar species burnt across 100% of its range according to point locations—photograph credit: Royal Botanic Gardens Victoria. (c) Phylogenetic tree of Australian plant families displaying the percentage of species burnt in each family according to data from point locations (inner circle of coloured tips) or range mapping (outer circle of coloured tips). The tree was built from the phylogeny contained in *V. Phylomaker* (Jin & Qian, 2019), which combines the seed plant phylogeny from Smith and Brown (2018) with the pteridophyte phylogeny from Zanne et al. (2014)

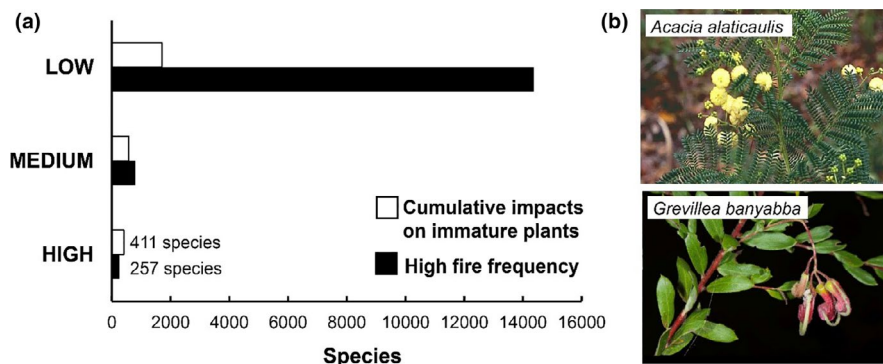


FIGURE 4 (a) Species ranked as high, medium and low risk of impact from the combined influence of the 2019–2020 fire season and two separate aspects of previous fire history: cumulative impacts on immature individuals (white) and high fire frequency (black); (b) both *Acacia alaticaulis* and *Grevillea banyabba* are obligate-seeding species with significant portions of their range burnt during and prior to the 2019–2020 fire season, leaving them vulnerable to the cumulative impacts of high fire frequency on immature plants. Photographs supplied from Worldwide Wattle/Terry Tame for *Acacia alaticaulis* and Andrew Orme for *Grevillea banyabba*

3.2 | Impacts on threatened plants

In total, 44% of all plant species already listed as threatened under national legislation (EPBC Act; $n = 587$ of 1,335) had some percentage of their range burned within the fire impact analysis area. This includes 44 species listed as Critically Endangered and a further 238

and 305 species, respectively, listed as Endangered and Vulnerable level. Of these 587 threatened plant species, 35 were burnt across $>90\%$ of their range, including the Critically Endangered shrub *Gastrolobium vestitum* (Domin) G. Chandler & Crisp (100% range burnt) and the annual herb *Gentiana bredboensis* L.G. Adams (96% range burnt).

Several Australian jurisdictions had large numbers of species listed as threatened under state legislation, which burned in the megafires (Table 1). Most notably, 386–598 of plant species listed as threatened under the NSW *Biodiversity Conservation Act 2016* had some portion of their range burnt, including 32–34 species burnt across >90% of their range ($n = 48$ unique species when combining range data across different sources). Seventeen of the 48 NSW threatened species with >90% range burnt are known to be killed by fire. These include *Zieria floydii* J.A. Armstr.—listed as Endangered on the NSW BC Act and EPBC Act—and *Pultenaea parrisiae* J.D. Briggs & Crisp—listed as Vulnerable on both Acts. The capacity of obligate-seeding species like these to recover from the 2019–2020 fire season will in part depend on previous fire history and future fire frequency (see *Species recovery potential relative to fire history*), as well as other threats present across the range. Similarly, in the state of Victoria—where 1,770 plant species were listed under the state *Flora and Fauna Guarantee Act 1988* as of June 2020—60%–93% of threatened plant species ($n = 963$ –1,499) had some portion of their range burnt. Although definitions and categories of threatened species vary between NSW and Victoria, these two states have the largest impact on their threatened plant species of any Australian jurisdictions (Table 1), although South Australia and Tasmania also have a high percentage of fire-affected threatened taxa.

3.3 | Impacts on Major Vegetation Groups (MVGs)

Several of Australia's MVGs were heavily impacted by 2019–2020 fires, including Eucalypt Tall Open Forest and Eucalypt Open Forests, which had 34% and 16% of their extent burnt, respectively (Table 3; Figure 1b). In total, 78,907 sq km of eucalyptus-dominated forest and woodland was burnt, including large areas of the Greater Blue Mountains World Heritage Area in NSW. Collectively, 62% of all the vegetation represented by the seven eucalypt-dominated MVGs was burnt (Table 3). A further 14% (3,384 sq km) of heath and shrublands were burnt.

Rainforests and Vine Thickets occur across a very small proportion of the Australian continent (0.5%), and 7.1% of this MVG (2,562 sq km) was burnt across the fire impact analysis area. Impacts on rainforest vegetation were concentrated in northern NSW and southern Queensland, including in a range of Gondwanan Rainforest World Heritage Areas. This MVG is fire-sensitive, and many of the constituent species are killed or have trunks that can slowly smoulder making the species very slow to recover from fire.

3.4 | Species recovery potential relative to fire history

In total, 595 plant species were considered to be at high risk of decline or local extinction from the 2019–2020 fire season due to either high fire frequency impacts or the cumulative impact of previous fires on immature individuals across their range, or both

TABLE 2 Impact of the 2019–2020 fire season on Australia's ten largest plant families

Family	Species (n)	Any range burnt (count)	Any range burnt (% species)
Fabaceae	3,304	2,132	65
Myrtaceae	3,055	2,058	67
Proteaceae	1,597	1,266	79
Asteraceae	1,404	1,034	74
Poaceae	1,232	807	66
Cyperaceae	957	662	69
Malvaceae	796	333	42
Rutaceae	694	536	77
Orchidaceae ^a	664	395	59
Ericaceae	660	515	78

Note: The number of species in each family, relative to the number with any burn across their range, is shown as a percentage. Numbers of species in each family were derived from accepted names in the Australian Plant Census. Estimates of the extent of the range burnt for species in each family are derived from both digitized herbarium records and range maps intersected with the National Indicative Aggregated Fire Extent database (NIAFED).

^aThe number of Australian orchids may be much higher; several orchid species names are not currently accepted in the Australian Plant Census.

risk factors ($n = 73$ species; Figure 4). This includes 257 species at high risk from high fire frequency that had $\geq 25\%$ of their range burnt in 2019–2020 and one or more previous fires within the fire impact analysis area in the last 5 years ($n = 13$ non-woody species) or 15 years ($n = 244$ woody species). Further, 411 obligate-seeding species were considered at high risk of poor recovery ($n = 37$ non-woody species; $n = 374$ woody species) as populations across $\geq 50\%$ of their range were likely in an immature or recovering state at the time of the 2019–2020 megafires. These species include the shrubs *Acacia alaticaulis* Kodala & Tindale, which was burnt across 100% of its range, and *Grevillea banyabba* Olde & Marriott, which is listed as Vulnerable on both the EPBC Act and NSW BC Act (Figure 4b).

Although most Australian plants burnt in the 2019–2020 fires were either not considered at risk from high fire frequency or cumulative risks to immature plants ($n = 8,235$) or had no data on fire response available for which these criteria could be assessed ($n = 15,136$ species, respectively), 798 and 571 plant species were ranked at medium risk from high fire frequency and cumulative risks to immature plants, and 14,368 and 1,710 as low risk, respectively (Figure 4). All data on burnt areas and risk rankings are provided in Appendix S2.

4 | DISCUSSION

Plant species were profoundly affected by Australia's 2019–2020 fire season, with both positive and negative implications. Of the 26,062 plant species assessed, we show that 17,197 had suitable

TABLE 3 Impact of the 2019–2020 fire season on Australia's Major Vegetation Groups (MVGs)

MVG code	Vegetation unit (MVG name)	Simplified vegetation unit	Area of MVG (% Australia)	Area of MVG burnt (%)	Area of MVG burnt (km ²)
6	Acacia Forests and Woodlands	Acacia-dominated	4.4	0.2	544
13	Acacia Open Woodlands	Acacia-dominated	5.0	0.001	2
16	Acacia Shrublands	Acacia-dominated	11.1	0.1	933
4	Eucalypt Low Open Forests	Eucalyptus-dominated	0.1	6.7	746
3	Eucalypt Open Forests	Eucalyptus-dominated	3.0	15.7	35,695
11	Eucalypt Open Woodlands	Eucalyptus-dominated	6.0	0.2	958
2	Eucalypt Tall Open Forests	Eucalyptus-dominated	0.5	33.8	12,016
5	Eucalypt Woodlands	Eucalyptus-dominated	11.1	2.8	23,847
14	Mallee Woodlands and Shrublands	Eucalyptus-dominated	2.8	2.7	5,644
12	Tropical Eucalypt Woodlands/Grasslands	Eucalyptus-dominated	1.8	0	0
20	Hummock Grasslands	Grasslands	17.8	0.1	1,124
19	Tussock Grasslands	Grasslands	6.8	0.04	217
21	Other Grasslands, Herblands, Sedgeland and Rushlands	Grasslands	0.6	0.7	324
22	Chenopod Shrublands, Samphire Shrublands and Forblands	Heath and shrublands	6.4	0.01	45
18	Heathlands	Heath and shrublands	0.2	12.1	1,894
15	Low Closed Forests and Tall Closed Shrublands	Heath and shrublands	0.2	1.2	225
17	Other Shrublands	Heath and shrublands	1.6	1.4	1,670
1	Rainforests and Vine Thickets	Rainforest	0.5	7.1	2,562
7	Callitris Forests and Woodlands	Woodlands	0.4	1.1	369
8	Casuarina Forests and Woodlands	Woodlands	0.2	1.0	156
9	Melaleuca Forests and Woodlands	Woodlands	1.0	0.3	237
10	Other Forests and Woodlands	Woodlands	0.6	1.2	522
22–33	Combined (e.g. cleared, modified, aquatic, unclassified)	Cleared/unclassified	17.8	11.6	11,909

Note: MVG data sourced from the National Vegetation Inventory System (NVIS; version 5.1). MVGs have been grouped into simplified vegetation units (e.g., Acacia-dominated). For simplicity, six MVGs were grouped into a single unit: cleared, non-native vegetation, buildings; inland aquatic—freshwater, salt lakes, lagoons; naturally bare—sand, rock, claypan, mudflat; mangroves; regrowth, modified native vegetation; sea and estuaries; unclassified forest; unclassified native vegetation; unknown/no data.

habitat burnt in the 2019–2020 bushfire season (69% of all species) and point locations from recent herbarium specimens confirm the presence of 9,092 of these species across their mapped habitat. Most impacted species have mechanisms to facilitate recovery after fire (e.g., resprouting capacity, seed banks protected from lethal fire effects), but high fire frequency will determine the impact on recovery potential and conservation outcomes. In total, 595 plant species may decline or become locally extinct following the 2019–2020 fire season due to the impact of high fire frequency or the threat of future fires during the recovery phase of immature individuals.

Fire impacts were widespread across Australian plant diversity, with affected species drawn from 245 of the 263 Australian plant families currently accepted in the APC. Eighty-one of these families had more than 50% of their species burnt. Of the 1,335 plant species listed as threatened on the EPBC Act, almost half (44%) had some range burnt ($n = 587$ of 1,335 species) including 44 Critically Endangered species, six of which were burnt across more than 90%

of their range. Of Australia's major vegetation groups, eucalypt-dominated forests had extensive areas burnt (78,907 sq km) and a significant proportion (7%) of fire-sensitive rainforest vegetation in the south of the continent was burnt, some of which may never recover or will need very long fire-free periods for recovery.

Our analyses show that the legacy effects of previous fires across species ranges will likely shape the potential for species to recover from the 2019–2020 fire season. High fire frequency—defined here as fires which recur at a location within a 5, 15 or 50-year period for non-woody, woody and rainforest tree species, respectively—may jeopardize recovery in at least 257 species. High fire frequency has previously been shown to cause mortality and limit recruitment in many Australian plant species and vegetation types (Keith et al., 2002; Wooller et al., 2002), and in many cases may result from management actions aimed at reducing fuel loads (Morrison et al., 1996). Although fire is an important element of the disturbance regime in Australian ecosystems, and many species have

evolved the capacity to regenerate effectively after fire, repeated burns across species ranges can lead to local extirpation of populations and increased global extinction risk (Wooller et al., 2002).

The risk of future fires occurring before populations of many obligate-seeding and fire-sensitive species affected by the 2019–2020 megafires have matured and replenished their seed banks threatens their long-term persistence. Our analysis of fire history data between 1969–2020 demonstrates that, for 411 obligate-seeding or fire-sensitive tree species, a fire in the next 5, 15 or 50 years anywhere across the documented range will likely increase extinction risk by killing immature plants and creating a net loss of individuals. Species with canopy seed banks are most at risk as these can be completely exhausted after a single fire event (Keith, 1996). Species with soil seed banks may have more resilience, but there may still be little to no seed bank remaining after a fire in some cases (Auld & Denham, 2006). Given that fire severity and frequency are both predicted to continue to increase under climate change (van Oldenborgh et al., 2020), several species may be driven to extinction in coming decades as fire-free periods are reduced (i.e., through interval squeeze; Enright et al., 2015).

The capacity for species to recover from fire is also shaped in part by the prevailing abiotic conditions across the range. For instance, individuals in productive environments associated with high precipitation or soil nutrients may have a greater capacity to regenerate post-fire relative to those in drier environments or on impoverished soils, or where drought conditions prevail either pre- or post-fire (Auld et al., 2020; Gallagher, 2020). We recognize that the analyses presented here do not take environmental variation into account when assessing species recovery potential. Future analyses may introduce more nuance by incorporating minimum fire return intervals, which are species-specific or aligned to recommendations for MVGs or calibrated to address productivity, aridity or land use gradients. Similarly, continued efforts to catalogue fire response traits (including primary and secondary juvenile periods) will decrease the uncertainty associated with the impacts of fire on species for which these data are lacking (Driscoll et al., 2010). Improving data on fire response traits and minimum fire return intervals requires a significant knowledge synthesis, which draws on extensive published literature, field studies and expert opinion. This synthesis was beyond the scope of our work in rapidly assessing fire impacts on plants but should emerge as a key goal for Australian science in response to the 2019–2020 fire season.

Although fire frequency and extent are critical elements of the fire regime which can determine the recovery potential of species, several other relevant features—including severity and seasonality—also shape the capacity for species to respond (Miller et al., 2019). For instance, many obligate-seeding species in Fabaceae are predicted to have low rates of germination in low severity fires (Auld & O'Connell, 1991; Palmer et al., 2018) and repeated “cool” burns may compromise recruitment in these species. Further, forests repeatedly burnt at very high severity can undergo structural change whether dominated by obligate-seeding species (Burrows & Middleton, 2016; Ooi et al., 2006) or species with a capacity to resprout (Ettchells et al., 2020; Prior et al., 2016).

The maintenance of “pyrodiveristy” via varying fire severity is thought to create a suite of different local and regional habitats for species survival (Kelly & Brotons, 2017; Tingley et al., 2016), though this idea has been challenged (Parr & Andersen, 2006). Fire severity varied markedly across the 2019–2020 fire extent (DAWE, 2020b), and it should be noted that low severity fires may be difficult to detect with satellite imagery. In some cases, high severity, stand-replacing fire occurred beside surface or sub-canopy fire creating a mosaic of impacts and subsequent recovery patterns. High severity fires are associated with topographic position and vegetation type (Ndalila et al., 2018), and these should be considered when stratifying monitoring programmes across species ranges.

4.1 | Field-based assessments are crucial for assessing recovery

Although the number of plant species with more than 90% of their range burnt is relatively low ($n = 90$ –153 species), the task of assessing post-fire recovery of these and other species is significant. Undertaking extinction risk assessments to assess decline and ongoing threats will be challenging for several reasons. Firstly, Australia is a large continent with many remote areas, which makes the distances and logistics required to undertake fieldwork simultaneously across multiple species difficult. Prioritization can assist in planning effective strategies for optimizing sampling, and resources can be coordinated nationally, or between state agencies, to minimize duplication of effort and increase data sharing (Southwell et al., 2020). Monitoring should also include lodging of voucher specimens with relevant herbaria to provide a long-term record of the species presence and important genetic material for conservation planning (Rossetto et al., 2021). Secondly, recovery will vary within and between sites and functional groups of species, increasing the need for repeat site visits, surveys across a representative proportion of species ranges and across diverse range of functional groups. The spatial distribution of post-fire abiotic conditions, in particular rainfall, may create a mosaic of recovery where some populations take longer to recover than others, or under some circumstances may not recover at all. Threats such as disease, herbivory, erosion and weed invasion may interact with direct fire impacts and with each other to create a cascade of hazards, which diminish or prevent natural recovery (Auld et al., 2020; Gallagher, 2020) and require management intervention. Given these challenges, an ongoing commitment to post-fire monitoring and management in the most fire-affected plant species will be essential for preventing local or global extinctions, which is of particular concern for Australian plants (Alfonzetti et al., 2021).

5 | CONCLUDING REMARKS

Australian species represent an important component of global plant diversity due to their endemism and evolutionary history and are a central component of Australian biodiversity. Although

many plant species will respond positively to the 2019–2020 fire season—recruiting new individuals from soil and canopy-stored seed banks—we have identified a significant cohort of plants, which urgently require field inspections of impacts and threats to natural recovery and may require targeted management to prevent population declines and extinction. As fires become more frequent, our capacity to rapidly respond and deploy management resources will need to sharpen. This includes revisiting approaches to prescribed burning practices, which impose area targets that ignore implications for biodiversity. To achieve this, scientists will need to continue to work collaboratively with other parts of society, including landholders and government, to further embed ecological knowledge into fire management in an increasingly pyric world.

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Peer Review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13265>.

DATA AVAILABILITY STATEMENT

Species-level data on the proportion of burnt area, endemic and threatened status, and risk ranking are provided in Appendix S2. Code and spatial data available from the corresponding author. The data that support the findings of this study are openly available in DRYAD at <https://doi.org/10.5061/dryad.76hdr7sw2>. [Correction added on 28 May 2021, after first online publication: Data Availability Statement has been updated.]

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BIOSKETCH

This team of researchers works collaboratively to support the assessment of the impacts of the 2019–2020 bushfire season on Australian plants, through desktop studies and on-ground management actions. We have combined expertise in biogeography, fire ecology, functional trait ecology, remote sensing and conservation biology.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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